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Short communication

Yellow plumage colour of Great Tits *Parus major* correlates with changing temperature and precipitation

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Weather is known to affect the phenology and behaviour of birds, but weather-related changes of phenotypic traits involved in communication have received little attention. Using an 8-year dataset, we investigated links between carotenoid-based reflectance of the freshly moulted breast of Great Tits *Parus major*, weather during the moulting period and food availability during the preceding breeding season, and we investigated interannual changes. In both sexes, we found a change of colour expression to more saturated and darker yellow over the study period in parallel with increasingly dry and warm weather during moult. These results indicate that the expression of traits playing roles in communication may be controlled by weather and may therefore shift in response to changing climate.

Keywords: carotenoid, communication, reflectance, signal

Owing to global climate change, the dynamics of biological systems in response to annual variability and systematic temporal shifts in environmental factors are in the spotlight. Birds are affected by these changes both directly (e.g. via physiological processes) and indirectly (mostly via food availability). For example, rainfall influences extra-pair copulation rate (Bouwman & Komdeur 2006), nestling body condition (Rodríguez & Bustamante 2003) and fledging success (Pasinelli 2001). Temperature is associated with reproductive timing (Bourret *et al.* 2015), brood size (Hušek & Adamík 2008) and provisioning rate (Redpath *et al.* 2002).

The above studies cover a broad spectrum of the consequences of weather variability for reproductive processes. In contrast, weather effects on signalling traits have received extremely little attention (for exceptions see Reudink *et al.* 2015, Järvistö *et al.* 2016, Warnock 2017). Furthermore, exploration of how these traits respond to across-year shifts in environmental conditions has largely been ignored, although variation in ornament expression at the population level could shape the intensity of sexual selection (Hegyi *et al.* 2007a).

Yellow breast feather reflectance in Great Tits *Parus major* is known to be an honest signal of individual quality (e.g. Hõrak *et al.* 2001, Senar *et al.* 2008, Broggi & Senar 2009, Hegyi *et al.* 2015) and may also be involved in sexual selection (Hegyi *et al.* 2007b, 2015). Yellow reflectance is greatly determined by carotenoids, which are obtained from the diet (Pagani-Núñez *et al.* 2014). Thus, carotenoid coloration can reflect nutritional condition during moult (Hill & Montgomerie 1994, Hegyi *et al.* 2015). Additionally, some attributes of yellow reflectance are also related to the amount of reflective feather surface (the matrix of keratin protein rods; Shawkey & Hill 2005). Nutrition, in turn, is determined by factors such as food availability and ability to hunt, which may depend on weather conditions (Avery & Krebs 1984). Therefore, here we used data collected over an 8-year period to assess whether yellow coloration in a Great Tit population in the Carpathian Basin varies with environmental changes by analysing associations between annual fluctuations in weather during moult and the expression of yellow breast feather reflectance. Additionally, as dietary carotenoids could be stored in tissues for months in some bird species (reviewed in McGraw 2006), we also analysed yellow colour in relation to caterpillar abundance during the preceding spring breeding season. Finally, we examined whether interannual trends in coloration could be linked to similar trends in weather conditions or food abundance.

METHODS

Data collection

Although some European populations of Great Tits could be partial and facultative vagrants, in Hungary most individuals are residents; across the year, 97.6% of recapture events occur within 5 km of the ringing site

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(Török 2009). At our study site (Pilis-Visegrádi Mountains, Hungary, 47°43′N, 19°01′E), Great Tits moult from early July to late September. Between 2005 and 2012, we captured birds in autumn (6 October to 27 November) using mist-nets. For the analyses, we used 168 females and 299 males after randomly excluding within-year or among-year repeat captures of individuals. Sex and age (yearling or older) were identified by plumage characteristics (Svensson 1992). We collected 10 breast feathers for each bird and stored them in envelopes in the dark until making spectrometric measures within 6 months of collection. We measured reflectance using a USB2000 spectrometer, DH-2000 light source, R400-7 detector and WS-1-SS white standard (Ocean Optics Europe, Duiven, the Netherlands). From each sample, we recorded three spectra with OOIBase32 software (Ocean Optics Europe). As we previously found for this population that achromatic intensity and relative chromatic intensity were the main sources of interindividual colour variation (Hegyi *et al.* 2007b), we calculated brightness (average intensity between 320 and 700 nm, $R_{320\text{-}700}$), UV chroma ($R_{320\text{-}400}/R_{320\text{-}700}$), yellow chroma ($(R_{700}–R_{450})/R_{700}$ (lower chroma values refer to lower UV or yellow saturation) and lutein absorbance (average log intensity/100 from 445 to 455 nm; lower value refers to higher lutein content). As measurement repeatability is high for this system, we averaged the three measurements for each individual. For more details and validation of spectral measurements, see Hegyi *et al.* (2015).

We collected caterpillar frass (using 12–15 collectors in the study plot, each 0.25 m^2) during the breeding seasons at regular intervals to estimate the peak abundance of caterpillars, the main food during breeding. We weighed the samples (to the nearest 0.001 g) and divided the mass values by the number of days between consecutive collections.

Weather data for July–September were acquired from the E-OBS gridded dataset (Haylock *et al.* 2008; European Climate Assessment & Dataset, http://www.ecad.eu) by extracting the time series for the gridcell representing the region 47.50°–47.75°N, 19°–19.25°E. We obtained the daily means of temperature and precipitation, and calculated arithmetic means for months.

Data analysis

To avoid multicollinearity, we applied principal components analyses (PCAs) to colour variables. We pooled the sexes because common PCA (Phillips & Arnold 1999) showed similar colour correlation structures in males and females (results not shown). We performed PCA with varimax rotation on weather data pooled for all respective months on a larger dataset (1982–2014) to improve the reliability of the principal component (PC) axes. We tested for relationships of plumage colour with weather and caterpillar peak abundance variables using generalized linear mixed models with backward stepwise model simplification, normal error and identity link, and Satterthwaite estimation for degrees of freedom, as implemented in GLIMMIX (SAS 8.02, SAS Institute, Cary, NC, USA), with colour PC1 (see Results) as the response variable. Year was fitted as a random effect, sex and age as fixed categorical effects, and weather PCs and caterpillar peak abundance as covariates. Two-way interactions of fixed factors with the covariates were also fitted.

To investigate the association of colour with year, colour PC1 was used as the response variable, sex and age as fixed, categorical effects, year as both random factor and covariate, and initial models included the sex × age, sex × year and age × year interactions. To reveal whether the association of coloration with weather is independent of interannual changes in coloration and weather, we conducted a PCA on weather data and year together. This produced PC axes of climate that were orthogonal to the temporal change. We then ran the above-described mixed model with the resulting four weather PCs. We examined associations of year with weather PCs and caterpillar peak abundance using Pearson's correlations. We checked for normality of variables and model residuals by QQ plots. These analyses and the PCAs were run in STATISTICA 7.0 (Statsoft, Inc., Tulsa, OK, USA).

RESULTS

PCAs on coloration resulted in one PC that explained 71.2% of the variance with high loadings (brightness: 0.81, UV chroma: 0.79, yellow chroma: −0.81, absorbance: −0.95); in other words, individuals with a lower PC score had lower brightness and higher saturation. The weather PCA yielded three PCs, each correlated with the temperature (positive loading, $r > 0.83$) and the precipitation (negative loading, $r < -0.54$) of a given month. A higher PC score equates to warmer and drier conditions in the respective month. PC1, PC2 and PC3 explained 27.6%, 26.6% and 17.85% of the total variance and represented August, September and July, respectively.

We detected a negative association between coloration and August weather PC (Table 1, Fig. 1), and a decline of colour PC across the study period (Table 2, Fig. 2a). The effect of August weather on colour remained the same when using an August weather PC orthogonal (i.e. independent) to year (i.e. high loadings with temperature (0.92) and precipitation (−0.84), low with year (0.16); see detailed results in the Supplemetary Online Material). The effect of the random factor for year was not significant in either analysis (both

$P > 0.05$). We found that August weather changed with year ($r = 0.84$, $P = 0.009$, $n = 8$; Fig. 2b). The other weather PCs and caterpillar peak did not show significant correlations with year (all $P > 0.29$).

DISCUSSION

We found that colour expression was associated with August weather. This accords with a peak in August in the number of Great Tits moulting their contour feathers at our study site (84.4% of birds captured in August were just replacing their breast feathers). Birds developed breast feathers with lower brightness and UV chroma, and higher yellow chroma when August weather was warmer and drier.

Because temperature negatively affects daily energy expenditure in Great Tits (Tinbergen & Dietz 1994), it could be an important factor during the energy-demanding process of feather growth (Lindström *et al.* 1993), especially as this time of the year is characterized by low body mass in Great Tits (Perrins 2012). In late summer, arthropods, which are the diet of the Great Tit in this period (Perrins 2012), are generally scarce in deciduous forests (e.g. Illera & Atienza 1995), and at lower temperatures arthropods are less active, which makes them more difficult to find (Avery & Krebs 1984). Additionally, waterlogged plumage has negative impacts on flight manoeuvrability and energy expenditure, and in rain birds may shelter instead of foraging (Kennedy 1970). In sum, wet and cool weather may result in reduced food intake. The correlated decrease in yellow chroma and increase in UV chroma and brightness when moulting in cool and rainy weather suggests that these three changes are jointly shaped by the low availability and resulting low feather concentrations of carotenoids. These results are supported by the observations in our population, as the expression of yellow breast colour appears to partly depend on condition during moult (Hegyi *et al.* 2015).

In the American Redstart *Setophaga ruticilla*, Reudink *et al.* (2015) also found that carotenoid-based colour changed in association with weather. However, in contrast to our results, birds that replaced plumage under high precipitation and low temperature developed red feathers with lower brightness and higher red saturation. This is a long-distance migratory species with different moulting phenology, so it faces different constraints of time and energy budget during moulting. Furthermore, its feathers contain markedly different types of carotenoids (McGraw *et al.* 2005) compared with Great Tit feathers (Senar *et al.* 2008), which could be associated with different diets and feeding strategies. In another study, Warnock (2017) found that non-migratory

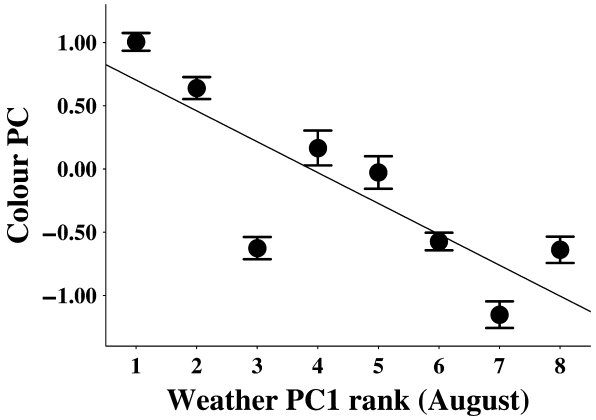

Figure 1. Relationships of yellow colour principal component (PC) with local weather PC1 in the Great Tit. Lower values of colour PC indicate more pigmented feathers with lower intensity and UV chroma and higher yellow saturation, whereas lower values of weather PC1 imply cooler and more rainy August. The figure shows the ranks of years according to the weather PC.

Table 2. Relationships of Great Tit yellow coloration to sex, age and year.

Effect	*F*	df	*P*
Sex	12.49	1, 462	0.0005
Age	0.11	1, 430	0.74
Year	48.29	1, 5.77	0.0005
Sex × age	0.09	1, 455	0.77
Sex × year	0.66	1, 462	0.42
Year × age	1.99	1, 316	0.16

Table 1. Relationships of Great Tit yellow coloration to sex, age, local weather and caterpillar peak abundance.

Effect	*F*	df	*P*
Sex	12.39	1, 460	0.0005
Age	0.00	1, 462	0.98
Weather PC1	14.72	1, 5.78	0.009
Weather PC2	0.24	1, 4.92	0.65
Weather PC3	0.13	1, 5.11	0.74
Caterpillar peak abundance	0.50	1, 4.8	0.51
Sex × weather PC1	0.39	1, 458	0.53
Sex × weather PC2	0.08	1, 459	0.78
Sex × weather PC3	2.10	1, 458	0.13
Sex × caterpillar peak abundance	1.45	1, 457	0.23
Age × weather PC1	0.91	1, 456	0.34
Age × weather PC2	0.08	1, 458	0.78
Age × weather PC3	0.00	1, 460	0.99
Age × caterpillar peak abundance	0.12	1, 460	0.73

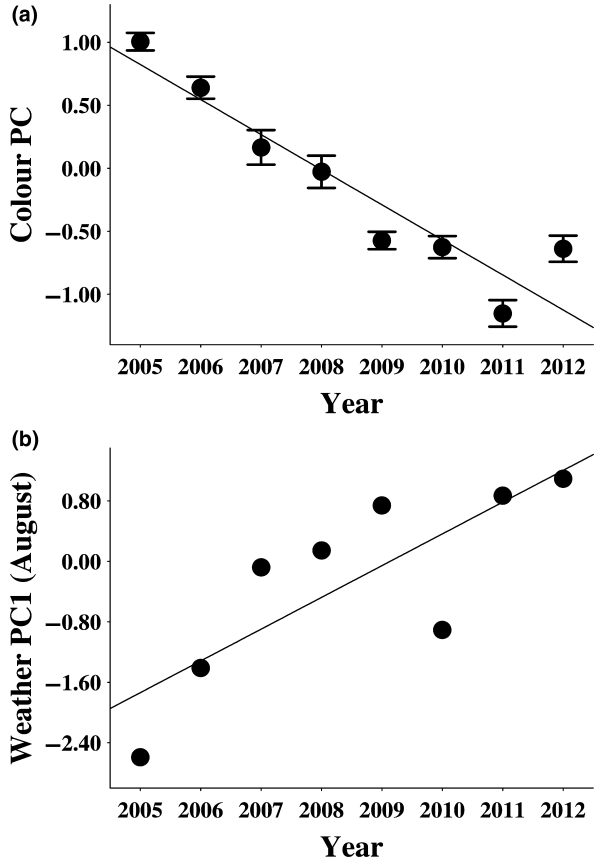

Figure 2. Interannual changes in (a) yellow colour principal component (PC) of Great Tits and (b) the local weather PC1. For explanations, see the legend to Figure 1.

Eastern Bluebirds *Sialia sialis* expressed more ornamented (brighter and more saturated) structural-based UV-blue plumage in breeding seasons after colder and wetter moulting seasons and, in females, the melanin-based pigment patch became lighter (less ornamented), which partially corroborates our findings. The differences between these and our results could arise from the very different colour-producing mechanisms of the plumage. Additionally, the bluebirds and redstarts occur at more southern latitudes during moult (American Redstart: 18°8′N; Eastern Bluebird: 32°5′N) with potentially different environmental constraints.

We found that colour production may not be sensitive to caterpillar peak abundance. This could be explained if carotenoids ingested several months before feather replacement were no longer available during moult (McGraw 2006).

We found that expression of yellow coloration systematically changed over the 8-year study period; Great Tits captured at the end of this period displayed darker and more saturated breasts. This systematic change could be the consequence of warming and drying Augusts over the years, which we also revealed here (see also August weather effects orthogonal to year in the Supplementary Material). Importantly, long-term climate change tendencies in the same direction have been described in the Carpathian Basin (Beuer *et al.* 2017). To date, there have only been a few studies that have investigated temporal changes in coloration at the population level and these have mostly been focused on longer (evolutionary) timescales. Using museum specimens, Warnock (2017) found that more recent Eastern Bluebirds displayed brighter UV-blue plumage, whereas melanin-based plumage reflectance showed no signs of change over a century. The other studies documented long-term trends for melanin-based colour-polymorphic species. Galeotti *et al.* (2009) found an increasing frequency of redness among Eurasian Scops Owls *Otus scops* over 137 years, and Karell *et al.* (2011) revealed an increase in the frequency of the darker morph of the Tawny Owl *Strix aluco* in a population in Finland over 28 years. Similarly, the proportion of brown colour forms in the Pied Flycatcher *Ficedula hypoleuca* in Finland decreased over a 54-year period (Sirkiä *et al.* 2013). Interestingly, in accordance with the latter finding, Järvistö *et al.* (2016) described that Pied Flycatchers displayed plumage with more coverage of melanic parts at both individual and population levels after winters with higher values of the North Atlantic Oscillation index (which means less moisture in the wintering grounds). It was later suggested that the above-mentioned temporal trends were adaptive responses to global climate change, as the darker colour morphs are more effective in thermoregulation and UV-protection (Roulin 2014). The above studies considered long-term trends and, other than Sirkiä *et al.* (2013), relied on museum specimens. Here we describe rapid directional change in a plumage colour trait in the field and directly link this to rapid climatic shifts in the same study area.

In summary, because carotenoid-based coloration often is an honest signal of the bearer's ability to find food, it has the potential to reflect changing environmental conditions through time, as suggested by our results. Further search for climate-induced ornamentation shifts is important because such shifts may abruptly impose strong selection pressures on sexual signalling systems.

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REFERENCES

Avery, M.I. & Krebs, J.R. 1984. Temperature and foraging success of Great Tits *Parus major* hunting for spiders. *Ibis* **126**: 33–38.

Beuer, H., Ács, F. & Skarbit, N. 2017. Climate change in Hungary during the twentieth century according to Feddema. *Theor. Appl. Climatol.* **127**: 853–863.

Bourret, A., Bélisle, M., Pelletier, F. & Garant, D. 2015. Multidimensional environmental influences on timing of breeding in a Tree Swallow population facing climate change. *Evol. Appl.* **8**: 933–944.

Bouwman, K.M. & Komdeur, J. 2006. Weather conditions affect levels of extra-pair paternity in the Reed Bunting *Emberiza schoeniclus*. *J. Avian Biol.* **37**: 238–244.

Broggi, J. & Senar, J.C. 2009. Brighter Great Tit parents build bigger nests. *Ibis* **151**: 588–591.

Galeotti, P., Rubolini, D., Sacchi, R. & Fasola, M. 2009. Global changes and animal phenotypic responses: melanin-based plumage redness of Scops Owls increased with temperature and rainfall during the last century. *Biol. Lett.* **5**: 532–534.

Haylock, M.R., Hofstra, N., Klein Tank, A.M.G., Klok, E.J., Jones, P.D. & New, M. 2008. A European daily high-resolution gridded dataset of surface temperature and precipitation. *J. Geophys. Res. Atmos.* **113**: D20119.

Hegyi, G., Török, J., Garamszegi, L.Z., Rosivall, B., Szöllősi, E. & Hargitai, R. 2007a. Dynamics of multiple sexual signals in relation to climatic conditions. *Evol. Ecol. Res.* **9**: 905–920.

Hegyi, G., Szigeti, B., Török, J. & Eens, M. 2007b. Melanin, carotenoid and structural plumage ornaments: information content and role in Great Tits *Parus major*. *J. Avian Biol.* **38**: 698–708.

Hegyi, G., Laczi, M., Nagy, G., Szász, E., Kötél, D. & Török, J. 2015. Stable correlation structure among multiple plumage colour traits: can they work as a single signal? *Biol. J. Linn. Soc.* **114**: 92–108.

Hill, G.E. & Montgomerie, R. 1994. Plumage colour signals nutritional condition in the House Finch. *Proc. R. Soc. Lond. B* **258**: 47–52.

Hõrak, P., Ots, I., Vellau, H., Spottiswoode, C. & Møller, A.P. 2001. Carotenoid-base plumage coloration reflects hemoparasite infection and local survival in breeding great tits. *Oecologia* **126**: 166–173.

Hušek, J. & Adamík, P. 2008. Long-term trends in the timing of breeding and brood size in the red-backed shrike *Lanius collurio* in the Czech Republic, 1964–2004. *J. Ornithol.* **149**: 97–103.

Illera, J.C. & Atienza, J.C. 1995. Foraging shifts by the Blue Tit (*Parus caeruleus*) in relation to arthropod availability in a mixed woodland during the spring-summer period. *Ardeola* **42**: 39–48.

Järvistö, P.E., Calhim, S., Schuett, W., Sirkiä, P.M., Velmala, W. & Laaksonen, T. 2016. Carry-over effects of conditions at the wintering grounds on breeding plumage signals in a migratory bird: roles of phenotypic plasticity and selection. *J. Evol. Biol.* **29**: 1569–1584.

Karell, P., Ahola, K., Karstinen, T., Valkama, J. & Brommer, J.E. 2011. Climate change drives microevolution in a wild bird. *Nat. Commun.* **2**: 208.

Kennedy, R.J. 1970. Direct effects of rain on birds: a review. *Br. Birds* **63**: 401–414.

Lindström, Å., Visser, G.H. & Daan, S. 1993. The energetic cost of feather synthesis is proportional to basal metabolic rate. *Physiol. Zool.* **66**: 490–510.

McGraw, K.J. 2006. Mechanics of carotenoid-based coloration. In Hill, G.E. & McGraw, K.J. (eds) *Bird Coloration, Vol I: Mechanisms and Measurements*: 175–294. Harvard: Harvard University Press.

McGraw, K.J., Hudon, J., Hill, G.E. & Parker, R.S. 2005. A simple and inexpensive chemical test for behavioral ecologists to determine the presence of carotenoid pigments in animal tissues. *Behav. Ecol. Sociobiol.* **57**: 391–397.

Pagani-Núñez, E., Uribe, F., Hernández-Gómez, S., Muñoz, G. & Senar, J.C. 2014. Habitat structure and prey composition generate contrasting effects on carotenoid-based coloration of Great Tit *Parus major* nestlings. *Biol. J. Linn. Soc.* **113**: 547–555.

Pasinelli, G. 2001. Breeding performance of the Middle Spotted Woodpecker *Dendrocopos medius* in relation to weather and territory quality. *Ardea* **89**: 353–361.

Perrins, C. 2012. *British Tits*. Collins New Naturalist Library, Book 62. London: HarperCollins UK.

Phillips, P.C. & Arnold, S.J. 1999. Hierarchical comparison of genetic variance-covariance matrices. I. Using the Flury hierarchy. *Evolution* **53**: 1506–1515.

Redpath, S.M., Arroyo, B.E., Etheridge, B., Leckie, F., Bouwman, K. & Thirgood, S.J. 2002. Temperature and hen harrier productivity: from local mechanisms to geographical patterns. *Ecography* **25**: 533–540.

Reudink, M.W., McKellar, A.E., Marini, K.L., McArthur, S.L., Marra, P.P. & Ratcliffe, L.M. 2015. Inter-annual variation in American Redstart (*Setophaga ruticilla*) plumage colour is associated with rainfall and temperature during moult: an 11-year study. *Oecologia* **178**: 161–173.

Rodríguez, C. & Bustamante, J. 2003. The effect of weather on Lesser Kestrel breeding success: can climate change explain historical population declines? *J. Anim. Ecol.* **72**: 793–810.

Roulin, A. 2014. Melanin-based colour polymorphism responding to climate change. *Glob. Change Biol.* **20**: 3344–3350.

Senar, J.C., Negro, J.J., Quesada, J., Ruiz, I. & Garrido, J. 2008. Two pieces of information in a single trait? The yellow breast of the Great Tit (*Parus major*) reflects both pigment acquisition and body condition. *Behaviour* **145**: 1195–1210.

Shawkey, M.D. & Hill, G.E. 2005. Carotenoids need structural colours to shine. *Biol. Lett.* **1**: 121–124.

Sirkiä, P.M., Virolainen, M., Lehikoinen, E. & Laaksonen, T. 2013. Fluctuating selection and immigration as determinants of the phenotypic composition of a population. *Oecologia* **173**: 305–317.

Svensson, L. 1992. *Identification Guide to European Passerines*, Vol. 4. Stockholm: Märstatryck.

Tinbergen, J.M. & Dietz, M.W. 1994. Parental energy expenditure during brood rearing in the Great Tit (*Parus major*) in relation to body mass, temperature, food availability and clutch size. *Funct. Ecol.* **5**: 563–572.

Török, J. 2009. Széncinege. In Csörgő, T., Karcza, Zs., Halmos, G., Magyar, G., Gyurácz, J., Szép, T., Bankovics,

A., Schmidt, A. & Schmidt, E. (eds) *Magyar Madárvonulási Atlasz*: 554–556. Budapest: Kossuth Kiadó.

Warnock, M.C. 2017. Variation in Plumage Coloration of Eastern Bluebirds (Sialis sialis) in Relation to Weather and Geography. Doctoral dissertation. Appalachian State University.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Yellow plumage colour of Great Tits correlates with changing temperature and precipitation.